

The first fossil leptofoenine wasp (Hymenoptera, Pteromalidae): A new species of *Leptofoenus* in Miocene amber from the Dominican Republic

Michael S. Engel

Division of Entomology (Paleoentomology), Natural History Museum, and Department of Ecology & Evolutionary Biology, University of Kansas, Lawrence, USA

urn:lsid:zoobank.org:author:3714A7FF-E19E-495A-AAF9-98D2F597B757

Corresponding author: Michael S. Engel (msengel@ku.edu)

Academic editor: Michael Ohl | Received 6 April 2009 | Accepted 25 June 2009 | Published 30 June 2009

urn:lsid:zoobank.org:pub:94FB118C-4FD6-49AB-ADA6-80313E2B6212

Citation: Engel MS (2009) The first fossil leptofoenine wasp (Hymenoptera, Pteromalidae): A new species of *Leptofoenus* in Miocene amber from the Dominican Republic. ZooKeys 13: 57-66. doi: 10.3897/zookeys.13.159

Abstract

The first fossil of the pteromalid subfamily Leptofoeninae Handlirsch is documented. *Leptofoenus pitfieldae* sp. n. is described and figured from a single male preserved in Early Miocene (Burdigalian) amber from the Dominican Republic. The fossil is compared with its modern congeners and comments generally provided on the taxonomy of the subfamily, including a key to the two genera.

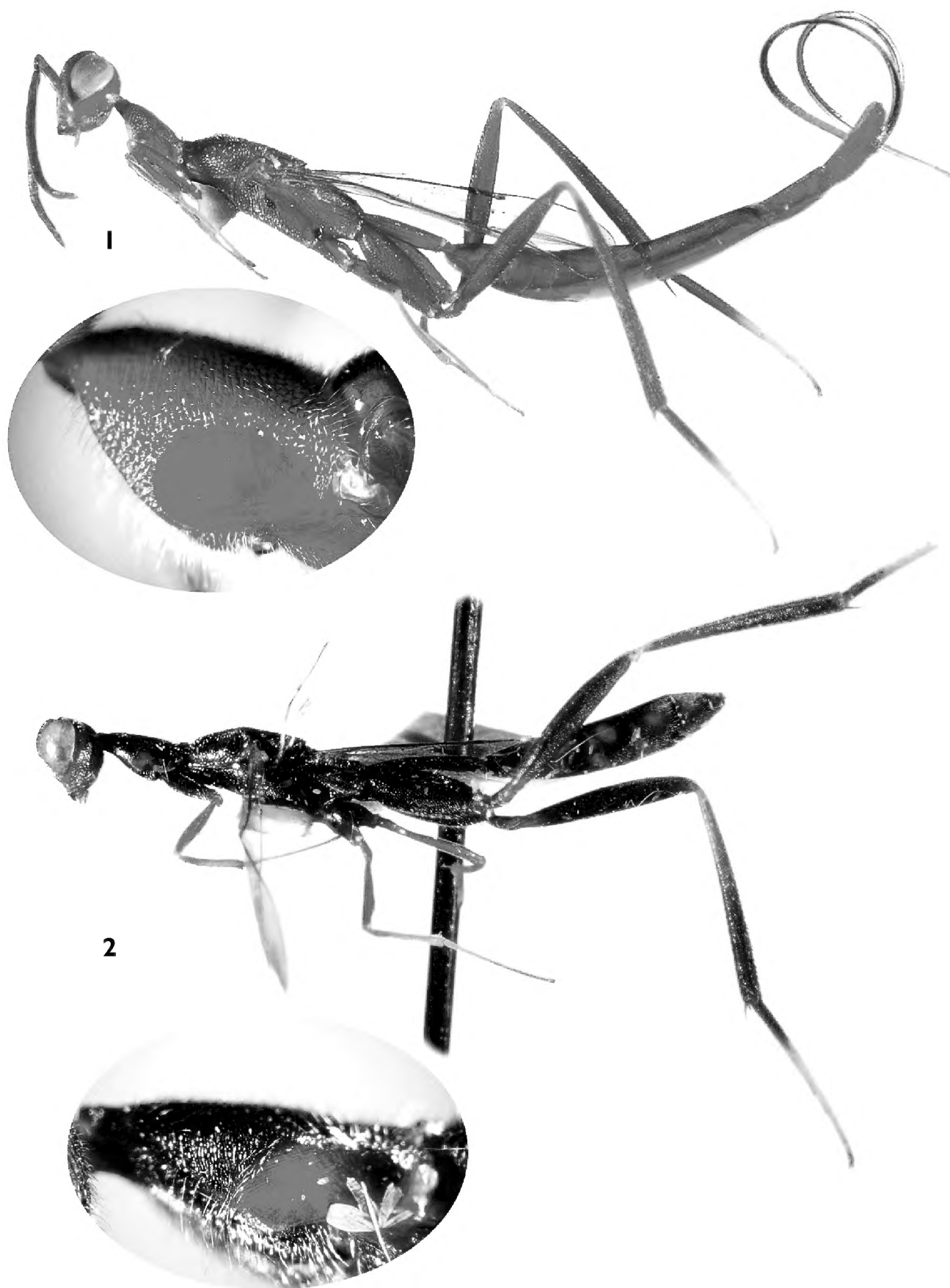
Keywords

Leptofoenus, taxonomy, paleontology, Pteromalidae, Chalcidoidea, Leptofoeninae, Miocene, Tertiary, amber, Dominican Republic

Introduction

The infrequently encountered wasps of the subfamily Leptofoeninae are remarkable giants among the otherwise more diminutive members of the Pteromalidae, a family that is likely paraphyletic, if not polyphyletic (e.g., Desjardins et al., 2007). With species ranging in size from 11-27 mm in females and 5-12 mm in males and their elongate, almost tubular body forms with elongate legs, leptofoenines closely resemble parasi-

toids of the Pelecinidae, Gasteruptiidae, and particularly the Stephanidae (Figs. 1-2), similarities reflected in the epithets for various species. When *Leptofoenus peleciniiformis* Smith was first described, Smith (1862) left open the familial assignment, reflecting this challenge in the name of the genus and species, the generic name implicating a placement near gasteruptiids and stephanids and the specific epithet indicating pelec-



Figures 1-2. Photomicrographs of representative modern *Leptofoenus* species and lateral aspects of their pronota. **1** *Leptofoenus rufus* LaSalle and Stage, female. **2** *Leptofoenus stephanoides* (Roman), male. Specimens from the collection of the Division of Entomology, University of Kansas Natural History Museum.

nids. Westwood (1868) subsequently described a separate genus and species, *Pelecinnella phantasma* Westwood, for what would later be recognized as a synonym of Smith's species, but he recognized the chalcidoid affinities of the group. Nearly 30 years later, Ashmead (1895) identified Westwood's genus as belonging to the Cleonymidae (today a subfamily of Pteromalidae) and established the subfamily Pelecinnellinae therein for this group. Handlirsch (1924), following Ashmead (1895), recognized Pelecinnellinae within the Cleonymidae, but placed *Leptofoenus* as a distinct family near the Stephanidae. Various authors treated Smith's and Westwood's genera as separate until 1924 when Brues recognized them to be synonyms and brought them together into a single group, employing Handlirsch's family-group name, Leptofoeninae, for the subfamily within Cleonymidae, a usage apparently followed by all subsequent authors (e.g., Bouček 1958, 1988; Hedqvist 1961), albeit sometimes at tribal rank.

Despite their conspicuous size nothing is known of leptofoenine biology aside from anecdotal notes that they have been collected from dead or fallen trees. Their structure is strikingly similar to wood-inhabiting stephanids, with elongate, tubular body; head with numerous tubercles on frons and vertex; long legs; mesopleural impression for reception of legs; elongate ovipositor; etc. The body form and structures are presumably adaptive for living in wood and being parasitoid on such boring insects as beetles and wood wasps, so it seems reasonable to suspect that leptofoenines have a similar biology. Two genera are presently recognized in the subfamily – *Leptofoenus* Smith, with five modern species in the New World ranging from northern Argentina to the southwestern United States, and *Doddifoenus* Bouček, with two species in Papua New Guinea and northeastern Australia (Table 1).

While fossils of the Pteromalidae have been recovered from various localities (e.g., Darling 1996; Gibson 2003), none have been hitherto found of the subfamily Leptofoeninae. Herein I described the first fossil leptofoenine from a male recently discovered in Early Miocene (Burdigalian) amber from the Dominican Republic (Fig. 3).

Table 1. Diversity and distribution of leptofoenine wasp species.

Species	Distribution
Genus <i>Doddifoenus</i> Bouček	
<i>Doddifoenus australiensis</i> (Dodd)	northeastern Australia
<i>Doddifoenus rex</i> Bouček	Papua New Guinea
Genus <i>Leptofoenus</i> Smith	
<i>Leptofoenus howardi</i> (Ashmead)	Paraguay, Brazil, Surinam
<i>Leptofoenus peleciniiformis</i> Smith	Brazil, Peru, Venezuela, Costa Rica
<i>Leptofoenus pittfieldae</i> Engel sp. n.	Dominican Republic (Early Miocene)
<i>Leptofoenus rufus</i> LaSalle & Stage	México, southwestern USA
<i>Leptofoenus stephanoides</i> (Roman)	Argentina, Paraguay, Brazil, French Guiana, Venezuela, Colombia, Panamá, Costa Rica, southern México
<i>Leptofoenus westwoodi</i> (Ashmead)	Argentina, Bolivia, Brazil, Peru, Venezuela, Guyana, Trinidad, Panamá

This is also the first leptofoenine recorded from the West Indies proper. Morphological terminology and format for the description generally follows that of LaSalle and Stage (1985) and Bouček (1988). Photomicrographs were prepared using a Nikon D1x digital camera attached to an Infinity® K-2 long-distance microscopic lens.

Systematic Paleontology

Family Pteromalidae Dalman, 1820

Subfamily Leptofoeninae Handlirsch, 1924

Pelecinellinae Ashmead, 1895: 231. Type genus: *Pelecinella* Westwood, 1868. Not to be given precedence over Leptofoenidae Handlirsch, 1924 in accordance with ICZN (1999, Art. 40.2).

Leptofoenidae Handlirsch, 1924: 744. Type genus: *Leptofoenus* Smith, 1862.

Diagnosis. Large, elongate species (5-27 mm in length); head subcubic, with paracrobal crests; inner orbits of compound eyes parallel or slightly divergent toward lower tangents; antenna 13-segmented (except see below), without true anellus, toruli situated above lower tangent of compound eyes; malar space short; mandible blunt, with large truncate apex, sometimes with a small ventral truncation or tooth; mesosoma elongate, with pronotum dorsally twice as long as wide; legs slender and elongate; petiole elongate; ovipositor elongate.

Comments. The family-group name based on *Pelecinella* predates that based on *Leptofoenus* and accordingly holds priority for usage. Although *Pelecinella* is a subjective junior synonym of *Leptofoenus* (Brues, 1924; LaSalle and Stage, 1985), this does not affect the availability of the family-group name based upon it (ICZN, 1999: Art. 40.1). However, reverting to Pelecinellinae for the subfamily is not in the general interest of nomenclatural stability given that a family-group name based on *Leptofoenus* has been in universal usage since at least 1958 (e.g., Bouček 1958). Accordingly, the name Leptofoeninae is retained as the name for this subfamily in accordance with the spirit, if not the precise letter, of Art. 40.2 (ICZN, 1999).

LaSalle and Stage (1985) provided a revision of the species of *Leptofoenus* [including at that time *Doddifoenus australiensis* (Dodd)], while Bouček (1988) characterized the two species of *Doddifoenus*.

Key to Genera of Leptofoeninae

- 1 Eighth gastral tergum reduced, represented by short rim posterior to apical margin of seventh gastral tergum; pronotal lateral surfaces posteriorly with finely striate regions (striolate area) of integument; basitarsus twice as long as second tarsomere (Argentina to southern United States).....***Leptofoenus* Smith**

- Eighth gastral tergum mobile, elongate and spike-like; pronotal lateral surfaces posteriorly with smooth regions of integument but distinctly no striolate region; basitarsus as long as or slightly shorter than second tarsomere (northeastern Australia, Papua New Guinea) ***Doddifoenus* Bouček**

Genus *Leptofoenus* Smith

Leptofoenus pittfieldae Engel, sp. n.

urn:lsid:zoobank.org:act:EA9AF9B8-EBBA-4F75-A447-99D0B2F3A3A5

Figs 3-5

Holotype. Male, KU-NHM-Ent DR-019; Early Miocene amber, Dominican Republic, La Toca group of mines northeast of Santiago, excavated in late Autumn 2008, Keith Luzzi coll.; deposited in the Insect Fossil Collection, Division of Entomology, University of Kansas Natural History Museum.

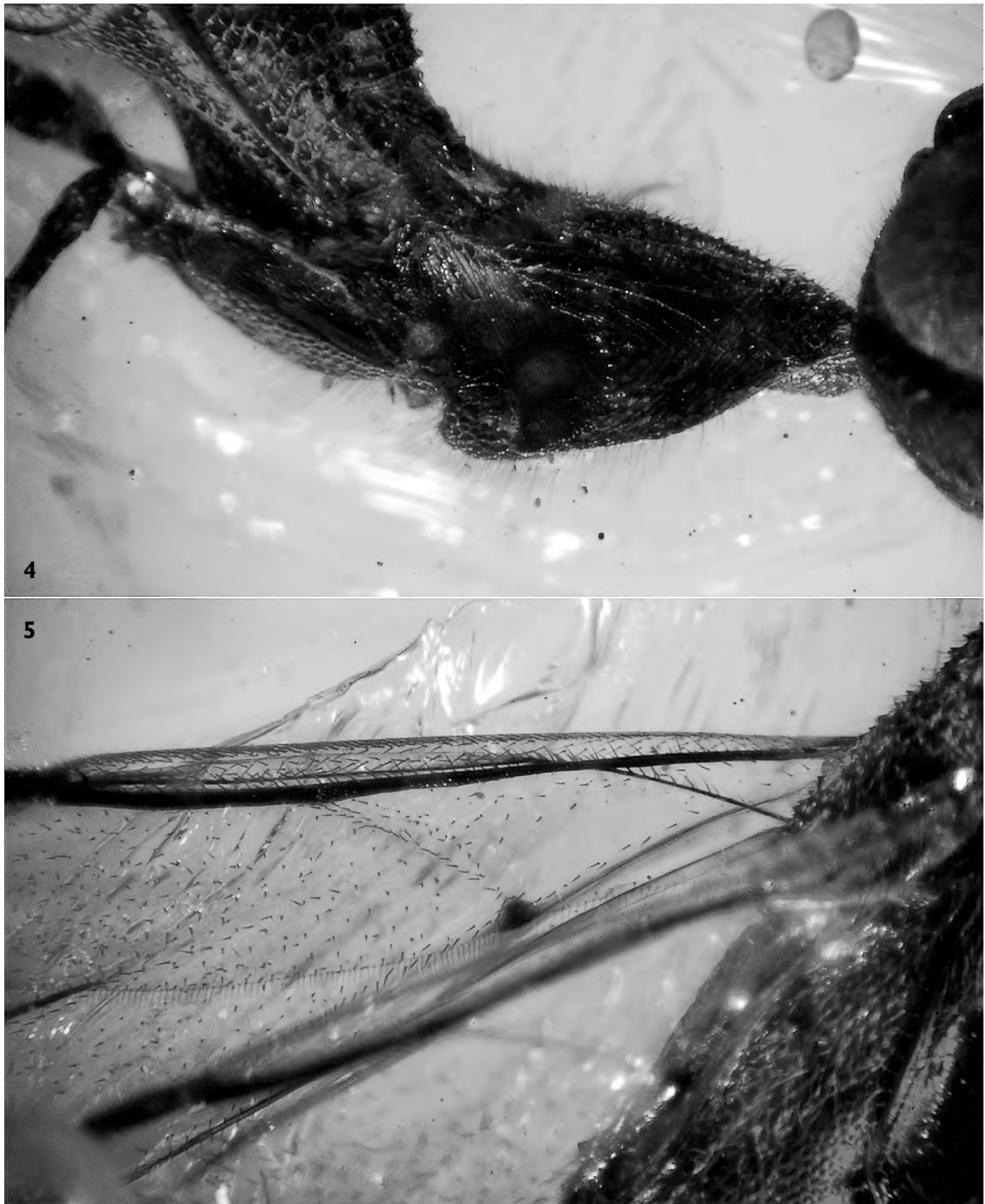
Diagnosis. The new species can be readily recognized from its modern and mainland congeners by the combination of a thinly sclerotized band posterior to M+Cu in the forewing (Fig. 5), the presence of a sclerotized spot in the forewing at the junction of M+Cu and the basal vein (Fig. 5), M+Cu being comprised of a series of 14 setae, the basal cell containing 22 setae, the anterior margin of the costal cell sclerotized with a dense fringe of short fuscous setae, the hind wing with only three hamuli, the apical-most antennal article apparently composite and resulting in an overall 11-segmented antenna, and the absence of a rasp-like structure on the inner surface of the metatibia.

Description. Male: Total length 8.8 mm; forewing length 4.7 mm; head 1.0 mm in length; mesosoma 3.3 mm in length, petiole 1.2 mm in length; gaster 3.3 mm in length. Integument dark brown throughout (Fig. 3). Head with scrobal cavity carinate laterally; maxillary palpus 4-segmented, apical palpomere elongate, with numerous elongate black setae dorsally; clypeus bare except for two erect setae laterally near oral fossa (visible in left, oblique view); antenna apparently 11-segmented, apical flagellar article elongate and apparently with lines indicating possible fusion of two very minute apical articles (resulting in an otherwise 13-segmented antenna); parascrobal crests and vertex strongly transversely striate, forming rasp-like structure dorsally. Mesosoma with pronotum and mesoscutum strongly, transversely strigate (Fig. 4), strigae increasingly bearing spicules posteriorly on mesoscutum; pronotum elongate, anterior margin rounded, posterolateral surface with striolate area (Fig. 4), striolate area ovoid (distinctly longer than wide; more rounded in *L. rufus* LaSalle and Stage), striations in striolate area finer and more evenly spaced anteriorly; mesoscutellum strongly transversely strigate, with numerous spicules; mesopleuron coarsely and irregularly punctate except in impressed region largely glabrous; propodeum laterally densely and contiguously punctate, with sparsely scattered setae. Procoxa with strong carina along dorsolateral margin; metacoxa sculptured as on lateral surface of propodeum; metafemur longitudinally striate ventrally except reticulate basally; metatibia without longitudinal rasp-like structure on inner surface; metabasitarsus twice as long as second tarsomere (tarsi pentamerous). Forewing with anterior margin of costal cell sclerotized (Fig.



Figure 3. *Leptofoenus pittfieldae* Engel sp. n. (KU DR-019), photomicrograph of male holotype (length of specimen 8.8 mm).

5), with dense fringe of short fuscous setae; basal cell with 22 setae; sclerotized spot at junction of M+Cu and basal vein (Fig. 5); M+Cu composed of series of 14 setae and posteriorly by thinly sclerotized band leading to sclerotized spot (Fig. 5); hind wing with three hamuli. Metasoma with petiole approximately 7 times longer than wide (direct dorsal view not possible so this is estimated); petiole weakly transversely strigate dorsally; gaster imbricate.



Figures 4-5. Photomicrographs of holotype male of *Leptofoenus pittfieldae* Engel sp. n. (KU DR-019). **4** Detail of lateral surface of pronotum showing posterior striolate region. **5** Basal third of forewing showing sclerotized spot and distribution of setae along M+Cu and within basal cell.

Etymology. The specific epithet is a matronym honoring Ms. Morgan Pittfield, enthusiast of all things adventurous when it comes to amber and niece of Keith Luzzi, who generously donated the holotype and permitted its study.

Discussion

Monophyly of *Leptofoenus* relative to *Doddifoenus* is supported by the presence of a striolate area on the posterior lateral surface of the pronotum (Figs. 1-2), a structure of uncertain function but resembling a stridulatory apparatus. *Doddifoenus* is supported by the apomorphic presence of a mobile, elongate, spike-like ninth metasomal tergum (= eighth gastral tergum). Placement of the fossil species within *Leptofoenus* is readily supported by the presence of this striolate region (Fig. 4), along with a long basitarsus relative to the second tarsomere. Relationships within *Leptofoenus* were tabulated by LaSalle and Stage (1985), who considered *L. peleciniiformis* as basal owing to the absence of a sclerotized spot at the M+Cu-basal vein junction in the forewing (within a more restricted *Leptofoenus* with *L. australiensis* removed, *sensu* Bouček, 1988) (Fig. 6). The species *L. howardi* (Ashmead), *L. westwoodi* (Ashmead), and *L. stephanoides* (Roman) were considered a clade owing to the presence of a rasp-like structure on the inner margin of the metatibia. *Leptofoenus rufus* was placed in an intermediate position (Fig. 6), plesiomorphically lacking the rasp-like structure, but sharing with the aforementioned clade the sclerotized spot in the forewing, as well as a medioapical incision on the sixth metasomal tergum (= seventh abdominal tergum, fifth gastral tergum). In regard to these characters, *L. pittfieldae* would be placed in a position similar to *L. rufus* owing to the presence of a sclerotized spot in the forewing, but lacking the rasp-like structure on the inner surface of the metatibia (Fig. 6). The sclerotized anterior margin to the costal cell would appear to be another feature of phylogenetic value in the genus. *Leptofoenus peleciniiformis* lacks a sclerotized anterior margin, as in *Doddifoenus*, while the anterior margin is sclerotized and bears a fringe of setae in *L. rufus*, *L. pittfieldae*, and the clade of *L. howardi*, *L. stephanoides*, and *L. westwoodi*.

The new species will run to couplet 4 in the key provided by LaSalle and Stage (1985) where it then intermingles the characters. The fossil species basically agrees with the second half of couplet 4 in all attributes except that, like *L. howardi*, the vein beneath the basal cell (M+Cu) is represented by a series of setae (8-18 in *L. howardi*, 14 in *L. pittfieldae*). Uniquely for the genus, in addition to numerous setae demarcating M+Cu, this vein is very thinly sclerotized posteriorly along its length leading up to the sclerotized spot at the junction of the basal vein and M+Cu (Fig. 5). Unlike the couplet for *L. howardi*, *L. pittfieldae* has three hamuli on the hind wing and the basal cell has less than 25 setae, albeit not as few as in *L. westwoodi* and *L. stephanoides* which have less than 20 each (*L. pittfieldae* has 22). The thinly sclerotized band along the posterior of M+Cu and the structure of the apicalmost antennal article are unique and also can serve to immediately distinguish *L. pittfieldae* from its congeners.

Given that this is the only such specimen known despite the volumes of Dominican amber inclusions that have been scrutinized in the last few decades, it would appear

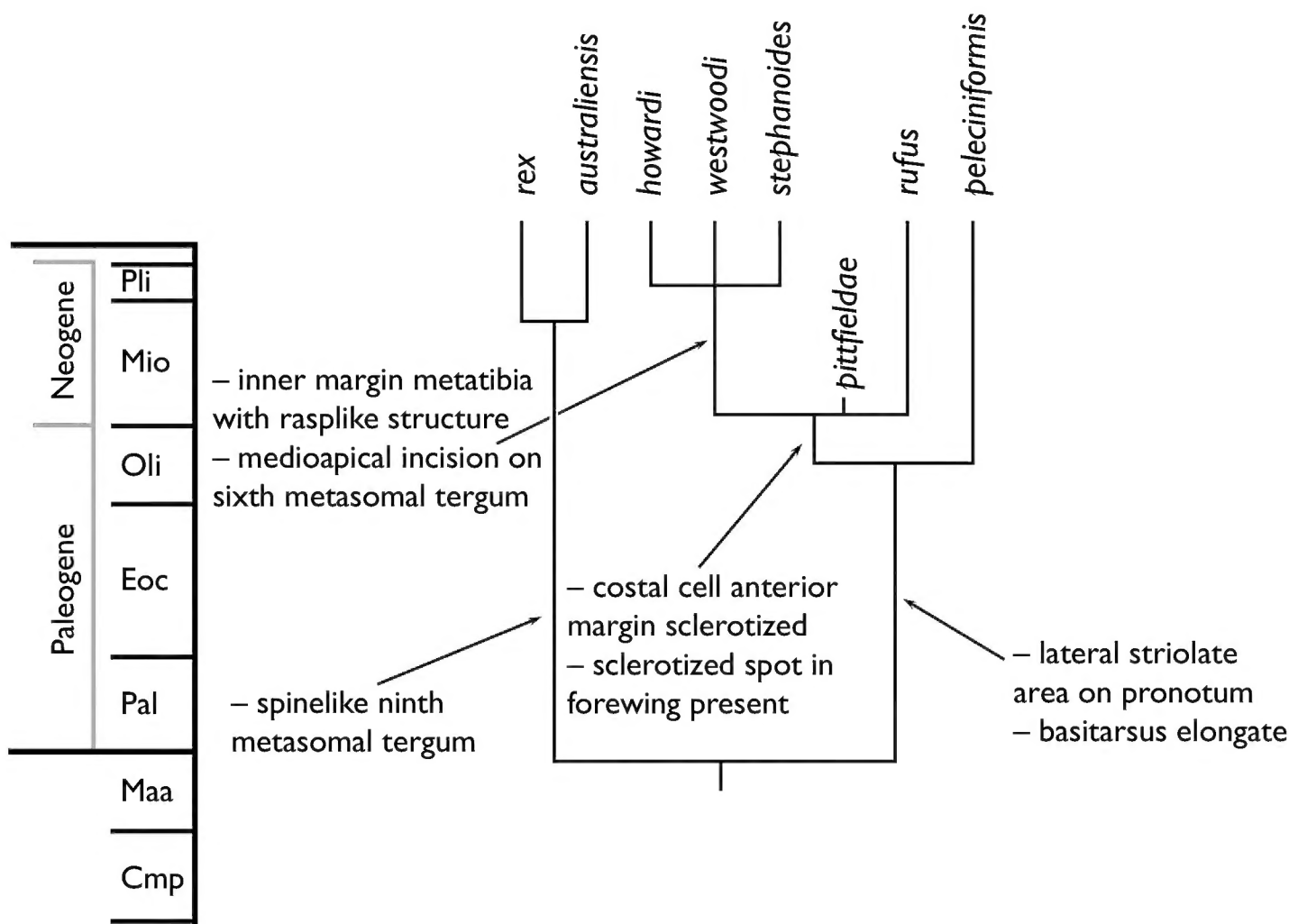


Figure 6. Phylogeny of Leptofoeninae, modified and expanded from LeSalle and Stage (1985).

that *Leptofoenus* occurred in as low abundance in the Miocene as they do today. *Leptofoenus pittfieldae* is the only leptofoenine documented from the West Indies. While such a geographic extinction would not be surprising given the number of localized extinctions documented from the Dominican amber fauna, it may not be a safe assumption that *Leptofoenus* is truly absent from the region. Given the rarity with which leptofoenines are represented in collections and the obviously large gaps in the distributions of the modern species (e.g., *L. stephanoides* ranging from northern Argentina to southern Mexico, yet not yet documented from several intervening countries such as Guatemala, Nicaragua, Honduras, or El Salvador), the possibility that the subfamily is today found somewhere across the various Caribbean islands cannot be immediately dismissed. Nonetheless, for the moment *L. pittfieldae* would appear to represent yet another group of insects which were established within the Miocene fauna of Hispaniola that subsequently became extinct.

Acknowledgements

I am grateful to Keith Luzzi for making the specimen described herein available for study and permitting its deposition in the Division of Entomology's research collec-

tion, and to David Grimaldi and an anonymous reviewer for insightful commentary on the manuscript. Partial support for this research was provided by U.S. National Science Foundation grants EF-0341724 and DEB-0542909. This is a contribution of the Division of Entomology, University of Kansas Natural History Museum.

References

- Ashmead WH (1895) On the genus *Pelecynella* Westwood, and its position among the Chalcididae. *Proceedings of the Entomological Society of Washington* 3(4): 230-233.
- Bouček Z (1958) Eine Cleonyminen-Studie; Bestimmungstabelle der Gattungen mit Beschreibungen und Notizen, eingeschlossen einige Eupelmidae (Hym. Chalcidoidea). *Acta Entomologica Musei Nationalis Pragae* 32: 353-404.
- Bouček Z (1988) Australasian Chalcidoidea (Hymenoptera): A Biosystematic Revision of Genera of Fourteen Families, with a Reclassification of Species. CAB International, Wallingford, [ii]+832 pp.
- Brues CT (1924) The identity of *Leptofoenus* F. Smith and *Pelecynella* Westwood (Hymenoptera). *Psyche* 31(6): 302-304.
- Dalman JW (1820) Försök till Uppställning af Insect-familjen Pteromalini, i synnerhet med afseende på de i Sverige funne Arter. *Fortsättning, Kungliga Svenska Vetenskapsakademiens Handlingar* 41: 340-385.
- Darling DC (1996) A new species of *Spalangiopecta* (Hymenoptera: Pteromalidae; Ceinae) from Dominican amber: Phylogenetic and biogeographic implications. *Journal of the Kansas Entomological Society, Supplement* 69(4): 248-259.
- Desjardins CA, Regier JC, Mitter C (2007) Phylogeny of pteromalid parasitic wasps (Hymenoptera: Pteromalidae): Initial evidence from four protein-coding genes. *Molecular Phylogenetics and Evolution* 45(2): 454-469.
- Gibson GAP (2003) Phylogenetics and classification of Cleonyminae (Hymenoptera: Chalcidoidea: Pteromalidae). *Memoirs on Entomology International* 16: v+1-339.
- Handlirsch A (1924) Systematische Übersicht. In: Schröder C (Ed) *Handbuch der Entomologie*, Band 3: Geschichte, Literatur, Technik, Paläontologie, Phylogenie, Systematik. Fischer, Jena, 377-1143 [total volume pages viii+1201 pp.].
- Hedqvist KJ (1961) Notes on Cleonymidae (Hym. Chalcidoidea), I. *Entomologisk Tidskrift* 82(1-2): 91-110.
- International Commission of Zoological Nomenclature (1999) *International Code of Zoological Nomenclature* [4th Edition]. International Trust for Zoological Nomenclature, London, xxix+306 pp.
- LaSalle J, Stage GI (1985) The chalcidoid genus *Leptofoenus* (Hymenoptera: Pteromalidae). *Systematic Entomology* 10(3): 285-298.
- Smith F (1862) Descriptions of new species of aculeate Hymenoptera, collected at Panama by R.W. Stretch, Esq., with a list of described species, and the various localities where they have previously occurred. *Transactions of the Entomological Society of London* 1: 29-44.
- Westwood JO (1868) Descriptions of new genera and species of Chalcididae. *Transactions of the Entomological Society of London* 7: xxxv-xxxvii.